BACTERIAL EXTRACELLULAR POLYSACCHARIDES

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In their natural environments, bacteria usually produce polysaccharides that coat their outer surface. Such polysaccharides are referred to as extracellular polysaccharide, exopolysaccharide, or EPS. Bacterial EPSs often are immunogenic. In vitro, the presence of EPS usually, but not always, is associated with a mucoid colony appearance on solid medium or with highly viscous culture broths. The coating of EPS on the bacterial outer surface sometimes is referred to as the glycocalyx (1) and can be in the form of a tightly held capsule or a loosely associated slime. Capsular EPS is attached to the cell surface by covalent bonding to either phospholipid or lipid-A molecules (2). Capsular EPS fibers can extend 3 μm or more from the bacterial cell surface as demonstrated by transmission electron microscopy. With few exceptions (e.g., curdlan), bacterial EPSs are water soluble and are highly hydrated, containing approximately 99% water (3).

EPSs are composed of sugar units connected to each other by glycosidic linkages. The majority of bacterial EPSs are heteropolysaccharides, which are comprised of regular oligosaccharide repeating units that normally contain two to six sugar moieties. A few bacterial EPSs, such as levan and dextran, are homopolysaccharides that consist of a single type of sugar. Most bacterial EPSs are of high molecular mass ($\geq$1 MDa) and carry a negative charge, although the majority of homopolysaccharides are neutral. A negative charge can be imparted by the presence of uronic acids or nonsugar substituents such as pyruvate, succinate, lactic acid, or phosphate (1,4,5). Some bacterial species produce a variety of EPSs. One example is *Escherichia coli*, which is known to synthesize over 80 different EPSs (6). Other species make only a very limited number of EPSs or even a single EPS.

Most genera of plant-pathogenic bacteria, including *Agrobacterium*, *Clavibacter*, *Erwinia*, *Pseudomonas*, *Pantoea*, *Ralstonia*, and *Xanthomonas*, produce EPSs (4). The complete structures of alginate, amylovoran, cellulose, levan, marginalan, stewartan, succinoglycan, and xanthan gum are known. Xanthan gum, produced by *Xanthomonas campestris*, is unique among the EPSs of plant-pathogenic bacteria as it is produced industrially in very large amounts for use in a variety of commercial food and nonfood applications (7).

Heteropolysaccharides are synthesized within the cell and then excreted past the bacterial outer membrane or cell wall. Intracellular synthesis involves (*1*) the synthesis of nucleotide sugar diphosphate intermediates, (*2*) assembly of the repeating oligosaccharide subunit by the transfer of monosaccharides from sugar nucleotides to the isoprenoid lipid carrier molecule, (*3*) addition of any nonsugar substituents, (*4*) transfer of the oligosaccharide subunit to the growing polysaccharide chain, and (*5*) export of the polymer to the extracellular environment (1). Thus many enzymes are required, some of which are also involved in the synthesis of lipopolysaccharides. The synthesis of the neutral homopolysaccharides levan and dextran is distinct. These EPSs are produced extracellularly solely by the action of the bacterial enzymes levansucrase or dextransucrase, respectively, on sucrose.

The structural and regulatory genes involved in EPS production can be either chromosomal or plasmid-borne. The regulation of EPS production is highly complex and involves both positive and negative regulators, some of which are global regulators that regulate the synthesis of other cell metabolites such as extracellular enzymes. Environmental signals, such as osmolarity and dehydration, may affect the synthesis of EPSs through the responses of two-component regulators (8). Often bacterial EPS production is favored by temperatures lower than those optimal for growth, a high carbon to nitrogen ratio in the growth medium and nutrient deprivation. Production of EPS also can be cell-density dependent because of quorum-sensing regulatory controls.

EPS production undoubtably plays important roles for the growth and survival of bacteria away from host tissues and in host–bacterial pathogen interactions. The EPSs protect bacteria from desiccation by forming a hydrated layer around the cell, act as ion-exchange resins binding nutrients and ions, mediate biofilm and microcolony formation, and act as adhesins in the attachment to a variety of surfaces (2,9). In addition, the EPSs of plant, human, and animal pathogens are known virulence factors (4,10–12). The EPSs of several plant-pathogenic bacteria are produced in planta and are important for bacterial colonization and subsequent prolonged water-soaking of host tissues and wilting of infected plants. Other possible roles include protection from plant antimicrobial defense compounds such as agglutinins and masking the presence of the invading bacteria from the plant host, thus preventing or delaying a hypersensitive response.

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